A Study of the Structure, Affinities, and Distribution of *Tetraplatia volitans* Busch (Coelenterata: Hydrozoa: Pteromedusae) [1]

CADET HAND [2]

INTRODUCTION

THE HYDROZOA include a large number of curious animals, not the least unusual of which are the tetraplatians. Two species of *Tetraplatia* have been described, *T. volitans* Busch (1851) and *T. chuni* Carlgren (1909). These hydromedusans are so highly modified in form that their true nature is seldom recognized when they are first encountered.

Tetraplatians are elongate (to 9.5 mm.) medusans of bipyramidal form with ciliated outer surfaces. The mouth lies at one extremity whereas the other end represents the aboral tip of the bell. In cross section the aboral region may be nearly cylindrical, quadrangular or octagonal while a cross section of the manubrium (oral end) may be circular to quadrangular. A constriction occurs near the middle of the body. In *Tetraplatia volitans* (Fig. 1) this constriction is bridged by flying-buttresses connecting the angular corners of the manubrium to the four major angles of the bell above the groove. These buttresses are absent in *T. chuni*. In the constriction and between the buttresses in *T. volitans*, and in a corresponding position in *T. chuni*, arise

four, bilobed, swimming appendages, the wings or lappets. Each lobe of each lappet has a statocyst. These lappets have a solid endodermal core (see Fig. 2). At the free extremity of the lappets there is a thin sheet of ectoderm which is interpreted as the velum; this velar structure may be continuous around the body in the constriction although not all specimens seem to show this. The lappets commonly have been called bilobed; however, at their free end 8 or 10 small velar projections can be found, four or five to each lobe. These projections are the result of at least three bifurcations of the supporting structure within the lappet, the first producing the bilobed appearance of the contracted lappet and the latter ones leading out to terminal velar projections of the lappets (Fig. 3). The surface of tetraplatians is marked by ridges, which are tracts of nematocysts; commonly the bell has eight tracts, four in the axes of the buttresses and four in the axes of the lappets, although those in the lappet axes may be absent. The manubrium never has more than four rows of nematocysts and these always are in the buttress axes.

Internally tetraplatians consist of a large, essentially quadrangular, gastrovascular cavity. The coelenteron extends into the buttresses from both the oral and aboral halves of the body. It has been reported that at the midpoint of the buttresses there may be a

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mesogleal septum separating the oral coelenteric pouch from the aboral (Carlgren, 1909) or that the passageway may be blocked by an endodermal plug (Dantan, 1925), although neither of these structures is necessarily present.

There are four gonads in the tetraplatians, each with an oral and an aboral bilobed portion. The gonads originate below the velum in the axes of the buttresses and project inside the animal, largely filling the coëlenteron when the animal is mature. The sexes are separate.

In summary, the tetraplatians are considered to be tentacleless medusans whose body is divisible into aboral and oral halves, separated by a line of tissue lying in the bottom of a constriction, this tissue representing the margin of the bell and the velum. The subumbrellar part of the animal is highly reduced and consists of only the manubrium and the tissues on the adoral surfaces of the lappets.

REVIEW OF RECORDED KNOWLEDGE

Tetraplatia volitans was first described by Busch (1851), presumably from a single specimen, taken at Málaga, Spain, in the Mediterranean Sea. He apparently observed the animal alive for a period of 2 days, and although he did not express an opinion on the nature or affinities of the animal, his description was good enough to enable subsequent authors to recognize it. Shortly after Busch's discovery, Krohn (1853) reported the finding of four specimens at Messina, Sicily. Twelve years later, having obtained no more specimens, Krohn (1865) published detailed observations on the four specimens he had obtained and suggested they must be young forms of some medusa (scyphozoan). Leuckart (1866), in considering the work of Krohn, suggested that *Tetraplatia* might be related to the medusan group of aeginids (now narcomedusans), and subsequently Claus (1878) in a very fine study established quite definitely the hydromedusan nature of the animal although at the same time he seemed to feel that it was half medusan and half polypoidal

and thus intermediate between polyps and medusae. Claus, however, used the name *Tetrapteron (Tetraplatia) volitans* for this species, and thereby created the first of the two recognized synonyms of *Tetraplatia volitans*, the second being that of Fewkes (1883) who used the name *Tetraptera volitans*. Haeckel (1879) in his "System der Medusen" suggested *Tetraplatia* might be a larval narcomedusan or that it might be intermediate between the hydroid polyps and the craspedote medusae. Fewkes (1883) in a brief note suggested that this curious animal might be best assigned a position between the craspedote medusae and the ctenophores. Viguier (1890), in an elaborate study of *Tetraplatia*, discussed the similarities of this animal to the trachymedusans, hydromedusans, larval actinians, scyphomedusans and ctenophores and seems to favor their relationship to the trachyline medusae. Perhaps the most careful and complete study of the tetraplatians is that of Carlgren (1909) based upon specimens from the Deutsche Tiefsee Expedition and also on specimens from Messina. From a single specimen from the west coast of Africa he described the species *T. chuni*, and after elaborate morphological and histological study of it and of specimens of *T. volitans*, Carlgren proposed a new order, the Pteromedusae, for *Tetraplatia*. This order represented a third group of trachyline medusae of equal rank to the Trachymedusae and Narcomedusae. Subsequent to Carlgren's study Krumbach (1924) decided that the tetraplatians were really larval animals in spite of their possession of well developed gonads, and placed them among the Scyphomedusae. In 1925 Dantan published a detailed study of *Tetraplatia volitans*. He disagreed with Carlgren's study on a number of points, perhaps the most important of which concerned the origin of the statocysts. Dantan maintained that these balance organs were of ectodermal origin, as opposed to the endodermal origin proposed by Carlgren, and after much discussion placed *Tetraplatia* among the Anthomedusae. Weill

(1934) in his study of the nematocysts of the coelenterates concluded from the figures of Viguier (1890) that *Tetraplatia* has a mono-cnidom of atrichous isorhizas and as such must be assigned to the Narcomedusae. Weill's opinion seems to have been completely accepted by Hyman (1940), and the trachyline affinities of this animal have been quite generally accepted among those who have actually worked with the animal except for Dantan (1925) and Komai (1939). Komai concluded that *Tetraplatia* is a primitive scyphozoan, close to the Cubomedusae and Stauromedusae.

The distribution of *Tetraplatia*, with the data included in the present report, is nearly world wide. The first *Tetraplatia* was taken in the Mediterranean Sea (Busch, 1851) and the next several reports of the animal were also from the Mediterranean concerning specimens taken at Messina. In 1885 Viguier reported finding specimens in the Bay of Algiers and his report of 1890 concerns the finding of these animals at that locality for five successive winters through a seasonal period from the end of December to the last of March and early April. Viguier was the first person to find *Tetraplatia* in large numbers and reported taking 200 specimens in a single net haul. Rose (1926) reported a single specimen from the Bay of Algiers. Carlgren (1909) extended the distribution of *T. volitans* to the neighborhood of the Chagos Islands in the Indian Ocean (4°5.8′ S., 73°24.8′ E.; 2°38.7′ S., 65°59.2′ E.) and also reported the single known specimen of *T. chuni* from the beginning of the Benguela current off the west coast of Africa at 36°23.4′ S., 17°38.1′ E. Dantan (1927) in a brief summary of the distribution of *T. volitans* reported it from the type locality of *T. chuni* but this was apparently an error. The next extension of known range occurred when Leloup (1935) reported the discovery of eight specimens of *T. volitans* from seven net hauls of the "Meteor" samples from the Atlantic (stations 41, 166, 183, 184, 216, 234, 278). These specimens ranged from 17° N. to 29° S. in the eastern Atlantic and
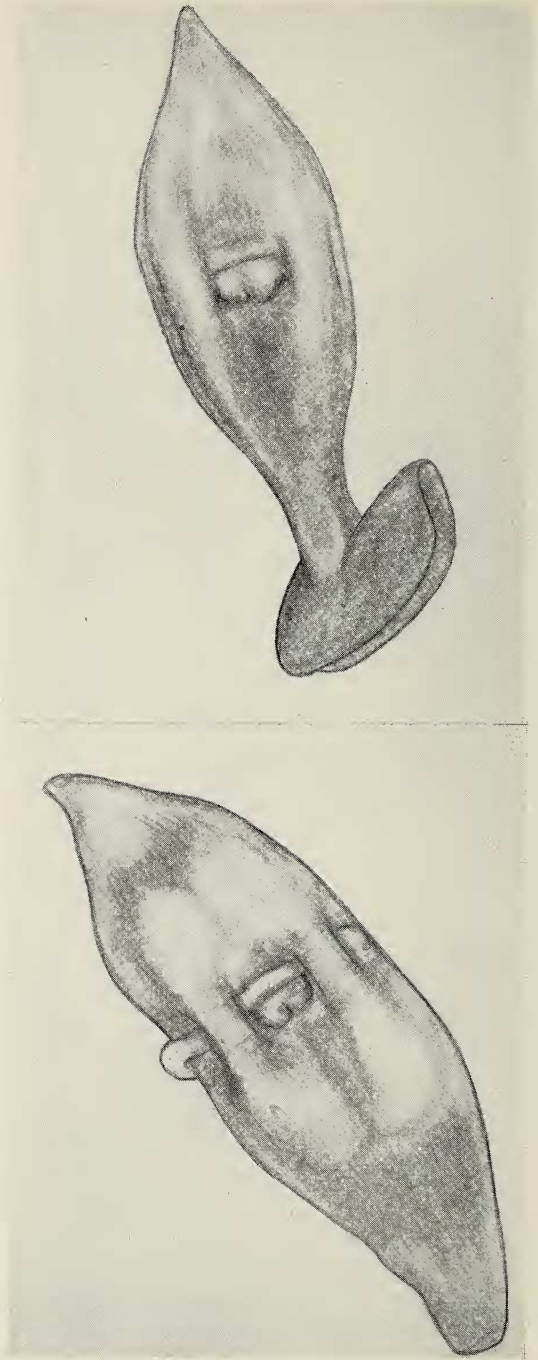

FIG. 1. *Tetraplatia volitans.* The upper specimen shows a widely flaring mouth and presumably was in the process of engulfing food at the time of fixation. (Carbon drawings by Mrs. Lois Stone, Department of Zoology, University of California, Berkeley.)

from about 23° to 30° S. in the western Atlantic (east and south from Rio de Janeiro, Brazil). Komai (1939) reported this animal from the Pacific for the first time. His report concerned four specimens taken in May at Susaki, Japan. Carlgren (personal communication) has informed me that he also has specimens from the western Pacific collected
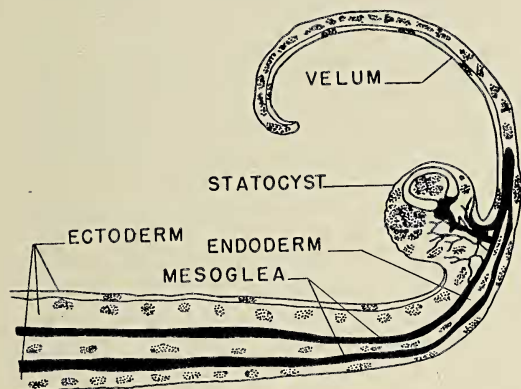

FIG. 2. Section through a lappet and statocyst, oral surface uppermost.

by the Dana expedition. The present report concerns the occurrence of *T. volitans* in the eastern Pacific. A total of 211 specimens has been found in 76 different net hauls from 44° N. to 5° S. and as far west as 131° W. The most northerly specimen was collected at 44° 12′ N., 128° 37′ W.; the most southerly at 5° 04′ S., 95° 56′ W. and the most westerly at 39° 38′ N., 131° 36′ W. Of the total specimens from the Pacific Ocean 167 were collected during the course of routine sampling by the Scripps Institution of Oceanography as part of the California Cooperative Sardine Research Program and also on its expedition "Shellback" to the eastern tropical Pacific. The remaining specimens (44) were collected in Monterey Bay, California, by personnel of Hopkins Marine Station during the course of their work on NC–ONR# 25127. Figure 4 shows the areas from which the specimens from the eastern Pacific were collected whereas Figure 5 indicates the world wide nature of the distribution of *T. volitans*. No specimens

have been reported from the Arctic or Antarctic regions, nor as yet from most of the southern and western Pacific.

The early workers on *Tetraplatia* commented but little upon its way of life. All the early specimens seem to have been taken in superficial net hauls and usually at night. Viguier (1890) thought they occurred "en petites troupes" and that they were the pelagic phase of a fixed or benthic animal. He points out that he did not find these animals associated with the truly pelagic (oceanic) forms. Carlgren (1909) was of the opinion that the tetraplatians were holoplanktonic. Dantan (1925), however, basing his conclusions on his observations of living animals, their movements and behavior, and on the spotty occurrence of these animals believed that they occur only accidentally in the plankton. He thought that they were not truly pelagic and that they lived near the bottom in rocky areas since net samples near sandy and muddy bottoms did not contain them. Dantan also disagreed with Viguier to the extent that when he (Dantan) found *Tetraplatia* it was in typical plankton assemblages. Leloup (1935) has taken an al-
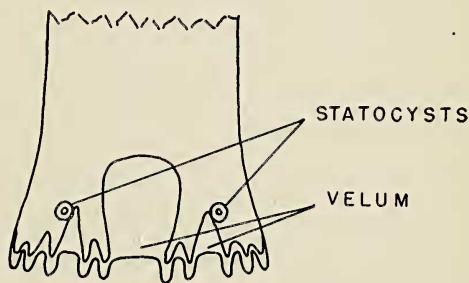

FIG. 3. Oral view of an expanded and flattened lappet.

together different point of view on the mode of life of this animal, and one to which I subscribe as will be seen in the observations and discussions to follow. He points out that the animals seem to be taken either in deep hauls during the day or in surface hauls during the night and suggests the animal must undergo a diurnal migration, coming to the

surface during the night. He also notes that whereas Dantan thought *Tetraplatia* must live near the bottom many specimens have been taken at distances several thousands of meters above the bottom.

As long as *Tetraplatia* was known from only the Mediterranean Sea it was thought of as an animal of rather regular seasonal occurrence. Viguier (1890) found it to occur from December to April and Carlgren (1909) reports that he was informed by letter that the season at Messina was from January to the end of July. The "Valdivia" material from the Indian Ocean was collected in February and March, while the "Meteor" specimens from the Atlantic were collected in March, April, July, October, and November. Carlgren's specimen of *T. chuni* was collected in November. Although the Mediterranean specimens still seem to appear only seasonally this is not true of the Atlantic material, which would appear to be present in all seasons. In the Pacific *Tetraplatia* has been found in samples taken in every month except January and presumably is present at all times of the year. Thus the problem remains of the apparent seasonality of occurrence in the Mediterranean and the apparent lack of seasonality in the Atlantic and Pacific, although samples from the latter two areas are too scanty to rule out seasonal periods of maximal and minimal abundances.

Most of the reports on *Tetraplatia* have dealt with it as a morphologic and systematic curiosity and very little is known of it as a living animal, except for the early studies of Busch, Krohn and Viguier. Dantan (1925) seems to have been the only recent worker to have studied it alive. The foregoing studies, however, give much information on its mode of swimming and the curious writhing movements which it undergoes, and the numerous excellent figures of Viguier (1890) show quite adequately the many shapes this medusa may assume. One interesting fact relative to the living *Tetraplatia* was the report by Viguier (1885) that the refringent bodies (statocysts)

were spontaneously luminescent and that they gave off a blue light. In his 1890 report, however, Viguier, after repeatedly seeking to confirm his earlier observation on the luminescence of the statocysts and having failed, suggests that what he observed may have been the result of the beginnings of the decomposition of the statocysts.

OBSERVATIONS ON PACIFIC MATERIAL

The 211 specimens of *Tetraplatia* which have been taken in the eastern Pacific have all been identified as *T. volitans* Busch. These specimens have an average size of 4.2 by 1.6 mm. and a range of from 1.0 by 0.6 mm. to 9.5 by 2.0 mm. The ratio of length to width approaches 1:1 in small contracted specimens although it is about 2:1 in most specimens less than 2.5 mm. long. Specimens of 3 mm. length and longer commonly have a length-
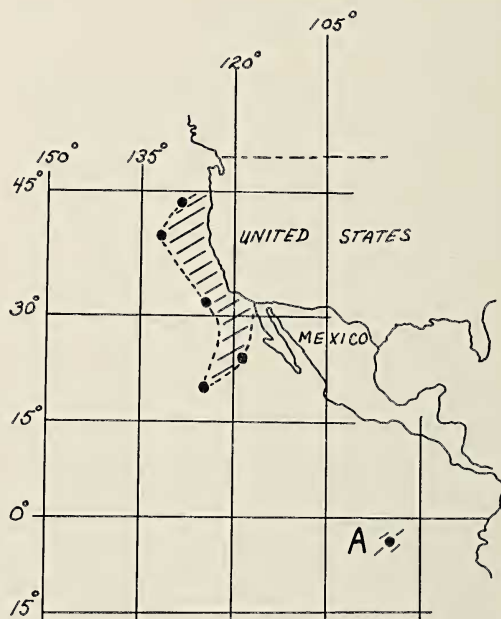

FIG. 4. Distribution of *Tetraplatia* in the eastern Pacific. Shaded area enclosed by dashed line indicates area from which *Tetraplatia* has been collected. The dot at A indicates the position from which the most southerly specimen was obtained, the dots on the dashed line represent the positions of collection of specimens which delimit the area within which most of the material was collected.
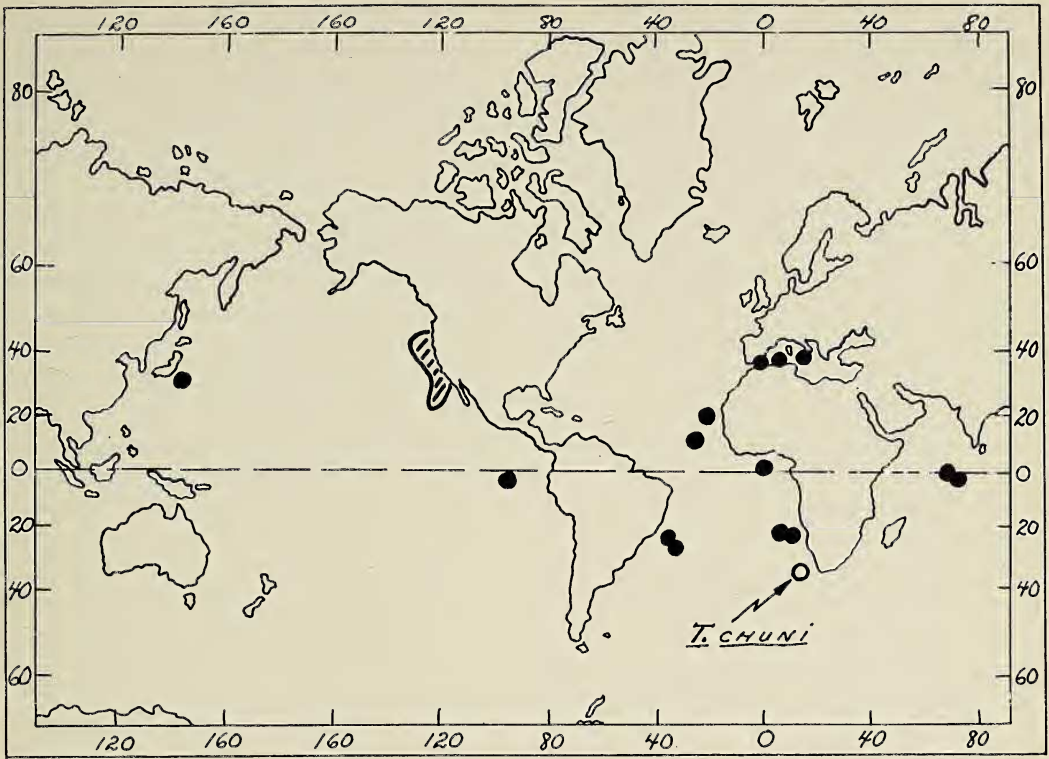
FIG. 5. Worldwide distribution of *Tetraplatia*. Dots and the shaded area in the northeastern Pacific represent localities which have produced *T. volitans*. The open circle is the locality from which *T. chuni* was collected.

to-width ratio of 3:1 with the very slenderest specimens having nearly a 5:1 ratio.

A number of specimens (12) were stained with borax carmine or rose bengal and subsequently cleared. One of the very obvious features of specimens so handled was the absence of the septum in the buttresses. Approximately at the midpoint of the buttresses there may be a slight thickening of the tissues, but in most specimens there was an open endodermal passageway from the oral to aboral coelenteron. In some of the buttresses this passageway seems to be closed off by the endodermal lining, although in six specimens which were prepared as serial sections no blockage was discovered. The passageway is not well formed, however, and consists of an irregular space lined by endoderm and at points along its course the endoderm cells nearly close it off. No sign whatsoever was seen of a mesogleal septum. Komai (1939) also reports the passageway as open, but Dantan and Carlgren, nonetheless, have reported this septum in material they have examined. It would seem therefore that the buttress canals may be closed by a mesogleal septum, an endodermal plug or, more commonly, contain an irregular endodermally lined canal. No special function can be assigned to the buttresses and their contained structures other than the obvious role the endodermal lining must play in the nutrition of the animal.

The presence of these buttresses is the character which most obviously separates *Tetraplatia volitans* from *T. chuni* which lacks these structures. It was therefore of great interest to discover that these structures are not constant and that on some specimens only two buttresses were present. Four spec-

imens were found which represented variations from the normal plan of four buttresses per animal. Figure 6a and b illustrate the first of these anomalies in which a buttress is nearly separated into halves, the halves apparently connected by only a thin piece of ectoderm. All other buttresses on this specimen were normal. A second anomalous specimen possessed only two buttresses; these were adjacent to one another and were normal in all respects. This specimen, however, possessed only three swimming plates and only the two buttresses just mentioned. Figure 6c and d illustrates this specimen. This specimen was triangular in cross-section except for the buttress missing from the side shown in Figure 6d. A third irregular specimen was one which possessed the normal four lappets but possessed only three buttresses, one being completely missing. The last anomaly was a specimen which also possessed four lappets, but only two buttresses, these being located 180° apart. This specimen is illustrated in Figure 6e and f.

Carlgren's T. chuni seems to be very little different from T. volitans, the major differences being the absence of the buttresses and the narrower lappets of his species as compared with T. volitans. In T. volitans the lappets, in general, are about as broad as the space between any two adjacent lappets, while in T. chuni the space between the lappets is about twice as wide as the lappets themselves. Our knowledge of T. chuni is based on a single specimen, 8 mm. long by 4 mm. wide, which by the standards of T. volitans is an unusually large, robust specimen. Careful measurements on the more robust specimens of T. volitans from the Pacific have indicated that the width relationships of the lappets to the space between lappets approaches the relationship of these measurements on T. chuni, but no specimen has been found whose lappets are quite as narrow as Carlgren described for his species. Also no specimen of T. volitans has been found which was as inflated as T. chuni and this in itself may account

for the differences observed. In T. volitans, as the specimens become greater in diameter (due largely to their state of expansion and contraction at the time of fixation), the width of the lappets becomes less as compared to the space between. It may be, therefore, that the presumed difference in relative widths of lappets between the two species is an artifact of preservation. As far as the difference in presence and absence of the buttresses between these two species is concerned it now is strongly suggested that this difference also may be an artifact, due in this case to a failure in the development of the buttresses. I do not choose, at this time, to
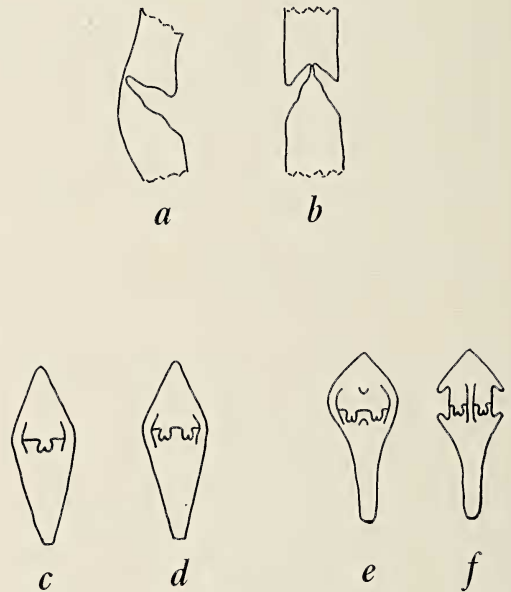

a   b

c   d   e   f

FIG. 6. Some aberrant *Tetraplatia volitans*. a, b, An incomplete buttress; c, d, a specimen with three lappets and two buttresses; e, f, a specimen with four lappets and two complete and two incomplete buttresses.

synonomize T. chuni with T. volitans, but such an act does not seem unwarranted. Another matter, which bears on this problem, concerns the geographic position from which T. chuni was collected (see Fig. 5). Carlgren's specimen came from the beginning of the Benguela current off the west coast of the tip of Africa, while in the same current, some 14° to the

north, Leloup obtained three specimens of *T. volitans* from the "Meteor" samples. From these facts it would not seem unreasonable to suggest again that *T. chuni* may be an aberrant specimen of *T. volitans*.

Among the many plankton samples examined I had the good fortune to discover specimens of *Tetraplatia* in a group of samples from horizontal, closing-net, tows taken in a vertical series. Four series of samples were taken at a single station (approximate position, 33° N., 117° W.) on the 4th and 5th of March, 1953. These consisted of two night series (2000–0330 hrs., 0400–0515 hrs. P.S.T.; the first series of 12 separate tows and the second series of only four separate tows) and two daylight series (1620–1820 hrs., 0615–1100 hrs. P.S.T.; the first of five tows and the second 11 tows). These tows were made with a net 1 meter in diameter, towed for 10 minutes. Table 1 indicates the length of wire used in each of the tows and the numbers of *Tetraplatia volitans* taken.

From the table it can seen that *Tetraplatia* was common in the first night series of samples and was absent from all others. These results agree very well with the suggestion of Leloup (1935) that *Tetraplatia* undergoes a diurnal vertical migration, approaching the surface only at night, except for the absence of specimens from the second night series. Sunrise, on the days when these samples were taken, was at approximately 0625 P.S.T. and during the time when the second series of night samples were taken the moon was slightly more than half illuminated and was nearly overhead. In the first night series no specimens were taken at the surface or at 10 meters depth while two and seven specimens were taken at 25 and 40 meters, respectively, so perhaps *Tetraplatia* was really absent from only the latter two hauls of the second night series. Also, since these latter two hauls were taken one hour and 45 minutes and one hour and 15 minutes, respectively before sunrise, it may well be that the *Tetraplatia* had already

TABLE 1

The Number of *Tetraplatia volitans* Taken in a Vertical Series of Horizontal Closing-Net Tows March 4 and 5, 1953

LENGTH OF WIRE OUT (METERS)	NIGHT SERIES		DAYLIGHT SERIES	
	No. 1	No. 2	No. 1	No. 2
Surface.......	0	0	0	0
10..........	0	0	0	0
25..........	2	0	0	0
40..........	7	0	0	0
60..........	4	**	**	0
80..........	3	**	**	0
100..........	2	**	*	0
150..........	0	**	**	0
200..........	1	**	**	*
300..........	0	**	**	*
400..........	..	**	**	*

* Net did not function properly.
** No sample taken.

begun their descent toward their daytime environment.

Excluding the 19 specimens collected in the series of hauls just reported, a total of 134 specimens has been recovered from 45 net hauls and of the 45 net hauls, only 12 were made during daylight hours. Of these 12 daylight samples, all but one were tows during which the net fished at depths greater than 300 meters, the exception being a tow whose greatest depth fished was approximately 70 meters. As compared to this single daylight haul which captured a single specimen, 15 night net hauls whose greatest depth reached was 70 meters produced a total of 19 specimens. The 11 remaining daylight tows which fished to depths greater than 300 meters produced a total of 79 specimens (1, 1, 1, 1, 2, 3, 7, 11, 16, 17 and 19 specimens per haul, respectively). With the exception of the haul which produced 16 specimens, these hauls were tows which fished from about 500 meters to 1,022 meters. The sample containing 16 specimens was a closing net tow taken at a depth of about 300 meters at 1455 P.S.T. From the data presented above it now seems to be apparent that *Tetraplatia volitans* is a

TABLE 2

THE NUMBER OF *Tetraplatia volitans* TAKEN IN A VERTICAL SERIES OF HORIZONTAL CLOSING-NET TOWS
JUNE 12 AND 13, 1952

NIGHT SERIES			DAYLIGHT SERIES		
Wire Out (Meters)	Time	Number of Specimens	Wire Out (Meters)	Time	Number of Specimens
10..........	2152	0	Surface.....	0913	0
4..........	2219	0	10........	0935	0
25..........	2253	0	25........	0955	0
40..........	2400	0	40........	1030	0
60..........	0029	1	80........	1130	0
100..........	0135	1	100........	1155	0
150..........	0205	1	150.......	1223	0
200..........	0243	1	200.......	1300	0
300..........	0325	1	300*.......	1340	0
400..........	0410	4	300........	1420	0
			400.......	1455	16

* Net did not close.

form which undergoes a diurnal vertical migration, approaching the surface at night and returning with the advent of sunrise to rather great depths. It should be pointed out that most of the samples of *Tetraplatia* which have been obtained were collected at positions where the depth to the bottom was greater than 1,000 meters and in many cases in water several thousand meters deep.

The sample mentioned above containing 16 specimens was one of a group of horizontal tows taken in a vertical series on June 12 and 13, 1952 at 33° 28.5′ N. by 117° 46.7′ W. *Tetraplatia volitans* was taken in seven of the 21 tows of this series (six tows of the night series and one of the day series). The results from this series of samples are shown in Table 2.

It will be noticed in this vertical series that by no means all of the specimens were taken near the surface at night, but instead they seem to be fairly evenly distributed over depths of about 40 to 300 meters (assuming a wire angle on these tows of about 45°). In the vertical series reported earlier in this study the center of the population, at night, seemed

to have been in the neighborhood of 40 meters. It therefore is apparent that although some tetraplatians undergo a marked vertical migration this is not necessarily the case, although these animals, almost without exception, descend to or stay at depths of 250 meters or more in the daytime.

Little information is available concerning the depths to which *Tetraplatia* may descend. Specimens have been recovered from samples in which the net fished from about 1,000 meters to the surface in the Pacific, while some of the "Meteor" specimens were taken in net hauls to depths of 900 meters and the "Valdivia" specimens to depths as great as 2,500 meters. However, since these net hauls were not closing-net tows, little but speculative results can be gleaned from them and no exact information is available concerning the lower limits of the vertical distribution of *Tetraplatia*. The 44 specimens from Monterey Bay add a little information along this line since it appears from the 11 tows which captured *Tetraplatia* that in general the deeper the tow the more specimens were captured. These tows were continuous from the depth

recorded to the surface and the number of specimens captured and depths reached were as follows:

Depth	Number of Specimens
510	1
620	2
775	1
846	3
870	2
890	2
960	4 (½ of sample only)
995	2
1,005	7
1,022	19
1,065	1

Tetraplatia, like most medusans, seems to be a rather omnivorous carnivore. Dantan (1925) seems to be the only other worker who has noted any of the food items of these animals and he found only a few specimens containing any identifiable food substances. He found the remains of an annelid larva, parts of a crustacean and a small chaetognath. In the specimens from the Pacific, also, only a few individuals have been noted containing identifiable food items. These included an immature euphausiid, a chaetognath and three copepods. Two specimens of *Tetraplatia* were noted whose mouths were widely flared,
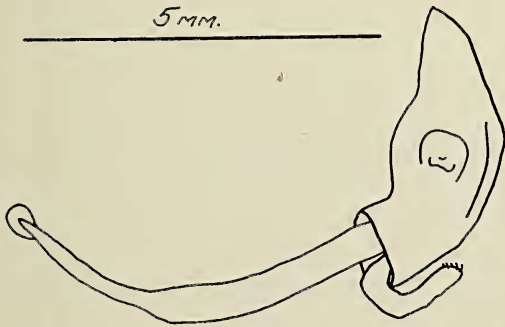
FIG. 7. A sketch of *Tetraplatia volitans* which had captured a chaetognath.

as if they had been attached to some rather large animal at the time of capture. An organism such as *Tetraplatia* can readily ingest another animal of its own bulk which was

nearly the situation with the specimen found ingesting the chaetognath. This individual with the partly swallowed arrow worm is sketched in Figure 7.

Nematocysts

Recently considerable attention has been turned toward the nematocysts of coelenterates. Weill (1934) used these structures to show phylogenetic relationships and Papen-
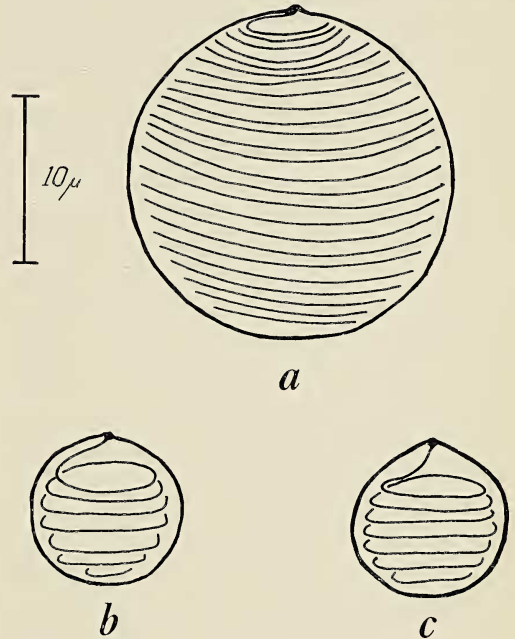
FIG. 8. Nematocysts of *Tetraplatia volitans*: *a*, a large atrich; *b* and *c*, small atrichs.

fuss (1936) and Hand (1954) have shown that these characters may be useful in the identification and separation of species. Russell (1938, p. 162) concurs with Weill that the study of nematocysts "may be of value in showing phylogenetic relationships," but questions their value as specific characters. In his elaborate study of 1934, Weill considered the nematocysts and affinities of *Tetraplatia volitans* and concluded that these animals were narcomedusans. He did not personally observe the nematocysts of this species but instead based his conclusions on the descriptions and figures of Viguier (1890).

Contrary to Viguier's opinion Weill felt that the variability in the size of the nematocyst capsules was insufficient to recognize more than one category—atrichs. In the present state of our knowledge the Narcomedusae, the group to which *Tetraplatia* was assigned by Weill, may be stated to have a mono-cnidom of atrichous isorhizas (atrichs).

I have examined twelve specimens of *Tetraplatia volitans* to determine the cnidom of this species as it exists in the eastern Pacific. Nematocysts are rare or absent from most of the body and are largely confined to the nematocyst tracts, although near the distal end of the manubrium the tracts become diffuse and nematocysts are generally distributed over this area. Only one type of nematocyst has been found in the tissues of *Tetraplatia*, this being an atrichous isorhiza, although two very obvious size categories are present. The smaller capsules appear to contain a coarser thread than the larger, and the thread in the larger capsule has many more coils than the smaller. Figure 8 illustrates the appearance of these atrichs. The capsules are all very nearly spherical, with some tendency to develop a low conical shape toward the opercular region, at least in the smaller ones. The large atrichs are restricted to the manubrium in their occurrence while the smaller occur throughout the nematocyst tracts. Dantan (1925) indicated that he too found a large and small type of nematocyst, although he gave very little indication of their structure. The sizes of the two categories of atrichs were as follows:

Small—8–12 μ diameter

Large—18–22 μ diameter

Komai (1939) also found two sizes of nematocyst, one 20 μ in diameter, the other 8 μ. He did not indicate what type nematocyst these were but his sizes agree well with what I have found.

Statocysts

Both Viguier (1890) and Dantan (1925), in their illustrations of whole *Tetraplatia*, have indicated the positions which the statocysts occupy. Carlgren (1909) has also described their location although he did not indicate their positions by figures. These writers seem to agree that the statocysts are located on the oral sides of the lappets, one in the middle of each of the two major lobes of the lappets at the junction of the velum and the lappet proper. Dantan had some difficulty in locating the statocysts, due to the more or less contracted and coiled-up condition of the flaps, and had to rely on sections to locate them. A number of the *Tetraplatia* from the Pacific have been examined in which the lappets were fully extended and in excellent states of preservation. As was remarked earlier, the term "bilobed" as applied to the lappets, is something of a misnomer since the lappets actually are divisible into at least eight terminal lobes. Moreover, the statocysts are not located at the midpoints of the two halves of the lappets, but are to be found just to the outer side of the second bifurcation of the supporting core of the lappets, as illustrated in Figure 3. The statocysts occur in a raised knob of tissue, and in sections it appears that the lithocytes have been derived from the endoderm. Figure 2 illustrates a section of a lappet through a statocyst.

In considering the structure of the lappets one feature appeared which was of considerable interest. This is the morphology of the nuclei of the velar and endodermal cells. The nuclei of the velum show a remarkable flattened and multilobed polymorphic structure, which is reminiscent of the nuclei of polymorphonuclear leucocytes. This is also true of some of the endodermal nuclei of the lappets which show a gradual transition from ovoid nuclei near the lappet base to the flattened, polymorphic type in the distal lappet endoderm. Dantan (1925) also noted these curious nuclei and Komai (1939) concluded that all of the cells possessing these polymorphic nuclei were endodermal.

The fully extended lappets of three specimens were constructed as is shown in Figure

3; that is, with the third bifurcation of the core of the lappet being wider on the outer than the inner side and with this lobe divided into two equal parts at its very tip. These lappets thus have ten terminal velar lobes. The fully extended lappets of three othe-specimens possessed unequal third bifurcar tions, but did not show the terminal division of the outermost lobe. The sizes of the spec-imens (3.2, 4.8, 5.0 mm.) which possessed ten velar projections were not significantly different from those which possessed only eight (2.4, 5.0, 5.2 mm.), and although one could easily assume that this variation in numbers of velar lobes is an age-correlated phenomenon it is not demonstrable as such from the data at hand. Attempts to determine the number of terminal velar lobes present on very small specimens (1 to 2 mm.) met with very desultory results. Most of these little animals possessed very tightly rolled lappets, and unrolling them is nearly impossible. On two specimens, however, it was possible to count eight terminal lobes on at least one lappet of each. The appearance of the division of the lateral terminal lobes, changing the number from eight to ten, may well be one which occurs fairly late in the development of these animals or may be a character which expresses itself in varying degrees.

DISCUSSION

Since Komai (1939) has so strongly es-poused the contention that *Tetraplatia* is a scyphozoan, considerable thought has been applied to test the basis for his conclusions. Komai has used the "octamerous arrange-ment of organs" and the "entodermal origin of the gonad" as features of a scyphozoan nature and has compared the lappets to the arms of stauromedusans. He makes a special point of identifying the structures usually con-sidered as the velum with the tentacles of the Stauromedusae and he points out that *Tetra-platia* also resembles the cubomedusans in its quadratic structure. Komai (1939, p. 248) finally concluded that ". . . *Tetraplatia* is a

primitive scyphozoon, retaining many char-acters of the actinula stage" and that ". . . the fins are probably a homologue of the marginal lappets of the ephyra, though more highly differentiated." Komai lists five lines of evi-dence which have been used by others to point to the hydrozoan nature of *Tetraplatia*. These lines are as follows: 1. the resemblance of the sense-organ to that of the trachymedusae; 2. the ectodermal gonads; 3. the presence of a velum; 4. the absence of septa and gastral filaments; 5. the absence of cells in the meso-glea. Komai agrees that the sense-organ is hydrozoan in nature and says (p. 245) that ". . . this may be the most questionable point of the scyphozoon theory." He states that items 2 and 3 above are "based on erroneous observations" and that 4 and 5 "are largely larval features." I cannot agree with Komai's conclusions and I feel that he himself has made some erroneous observations and inter-pretations.

The sense organ (statocyst) of *Tetraplatia* clearly is hydrozoan in nature; this Komai readily admits although he refers to the litho-style as a rhopalium. The origin of the gonads, although not observed as a developmental phenomenon, seems from a study of histo-logical preparations to be clearly ectodermal. It is true that the gonads have invaded the coelenteron to the extent that they occur embedded in ridges of endodermal tissue but they can be seen to be covered with meso-gleal tissue which separates them from the endoderm. Komai illustrates the position of the gonads where they approach the surface at the margin and shows the gonadial tissue covered by a thin layer of ectoderm. There is no indication of any mesoglea between the gonad and ectoderm but he says that mesoglea is inserted between the ectoderm and gonads. Among the six specimens, prepared as serial sections which I studied, five were ripe or nearly ripe adults (four females, one male) and one was an unripe immature individual of undeterminable sex. In the ripe specimens there is a very definite indentation or "pore"

at the point where the gonads contact the surface (behind the buttresses and immediately below the marginal band), and in the male groups of sperm cells were in these pores, and in one female a large ripe egg was half in and half out of one of the pores. In the immature specimen there is a gradual change in cell type from the ectodermal cells to the gonadial cells at the points where the gonads reach the margin. There is no mesoglea separating the ectoderm from the gonad at this point nor is there a definite epithelial layer covering the gonad as indicated by Komai. The conclusion from this is inescapable and obvious that the gonad is ectodermal and is derived as an ingrowth of epithelial ectodermal tissue into the endoderm, carrying with it the mesoglea which encases the adult gonad.

The matter of the presence of a velum is a very difficult point. The hydrozoan velum is a solid structure consisting of two layers of ectoderm separated by mesoglea. The mesoglea may, however, be nearly nonexistent judging from illustrations of velar anatomy of many hydrozoans and indeed the demonstration of mesogleal tissue in an animal like *Hydra* is not simple. Komai has interpreted what Carlgren and Dantan have called *velum* as tentacles and described and drawn them as being composed of a core of polymorphonuclear endodermal cells covered by epithelial cells. I find two details wrong with this conclusion. First the polymorphonuclear cells are not endodermal, but are ectodermal and second these are not tentacles but are part of the velar sheet, two cells thick, the cells of the oral side being thin, flat epithelial cells while the aboral surface is the layer of polymorphonuclear cells. I cannot determine if there is any mesoglea present between these cell layers. In the slides I have examined some sections, through tightly rolled lappets, were rather similar to Komai's figure 9 (Komai 1939, p. 240), but this appearance is the result of the rolling and folding of the velum. In expanded lappets there clearly are no adoral

appendages which could be interpreted as Komai has or which occur in the position Komai has indicated. Indeed, I find Komai's whole interpretation of the structure of the lappets to be incorrect. He has indicated that the lappets have on their oral surface a thin epithelial layer, next below this a layer of endodermal motor (muscular) cells with fibrous bases, below these another layer of endoderm (these contain the polymorphic nuclei), next the thick mesogleal layer which supports the lappets and then finally the outer-most layer of thin epithelium on the aboral surface. I find all these structures but cannot subscribe to his interpretations. There is a thin epithelial layer overlying a muscular layer on the oral surface of the lappets; however, both these tissues are ectodermal and are separated from the next layer, the endoderm, not by the fibrous bases of the motor cells but by a thin fibrous layer of mesoglea. A double sub-umbrellar layer of ectoderm is not an unknown feature in the Hydrozoa, the innermost layer being the muscular one. That the layer possessing polymorphonuclear cells is endodermal I do not question, since this layer can be traced through the serial sections and its confluence with the endoderm of the coelenteron is clear. Also the polymorphic nuclei gradually become regular ovoid nuclei near the base of the lappet and become identical in structure to those of the endoderm proper. The thickened aboral layer of mesoglea is a clear-cut structure as is the outer, aboral ephithelium and on their nature Komai and I agree. In my slides it is clear, however, that it is this latter, ectodermal, layer which gives rise to the cells with polymorphic nuclei of the velum and there appears to be no possibility that this could be an endodermal tissue in spite of the similarity of its nuclei and those of part of the endoderm.

Komai dismissed the absence of septa, gastric filaments and cells in the mesoglea as larval features. In the Scyphozoa the septa are well developed in the scyphistoma larva while the cellular mesoglea and gastric fila-

ments make their appearance in the ephyra. Since Komai suggests the "fins" or lappets are the same as those of the ephyra, it seems curious that he could so readily dismiss the absence of these other structures in this animal, *Tetraplatia*, even though he concludes it is neotenic.

I find that I am in complete disagreement with Komai and can only conclude that he has not properly interpreted the structure of this hydrozoan. One further point might be mentioned, however, before the hydrozoan nature of this animal is assured and this concerns the nematocysts. Scyphozoans quite generally possess atrichs, although they, as well, also possess at least one other type, even in the earliest developmental stages (Weill, 1934). This would seem to be further proof that *Tetraplatia* is a hydrozoan, since its cnidom is identical to that of the Narcomedusae. There are certain gross characters of *Tetraplatia* which do suggest the Cubomedusae, and some such organism as *Tetraplatia* conceivably could have been involved in the early evolution of the scyphozoan line, although *Tetraplatia* is clearly a hydrozoan. The problem which now must be solved is, "Where among the Hydrozoa should *Tetraplatia* be placed?" I believe *Tetraplatia* is a trachyline medusa and will now discuss this.

The trachyline medusae are commonly considered to be composed of two orders, the Trachymedusae and the Narcomedusae. The Trachymedusae are defined as possessing free or enclosed lithostyles containing endodermal lithocytes, a simple bell margin and a monocnidom of microbasic euryteles. The Narcomedusae on the other hand possess only free lithostyles, a scalloped bell margin and a monocnidom of atrichous isorhizas. The Narcomedusae also lack a true manubrium and may have peronia and otoporpae. The life histories of the trachylines as a whole lack a polypoid generation and are said to be direct, involving a planula, an actinula, and the adult. The gonads of the trachylines are sub-umbrellar and occupy a position either below the radial canals or in the floor of the stomach pouches (Narcomedusae).

Tetraplatia has a number of characteristics which suggest its affinities to the trachyline medusae and especially to the Narcomedusae. Its swimming plates or lappets can be homologized with the lappets of Narcomedusae as can the adoral stomach pouches which run into the buttresses. Its nematocysts are also narcomedusan. Its sensory structures, the statocysts (enclosed lithostyles), however, are trachymedusan. The position of the statocysts on the adoral lappet surface is, however, an unusual position since all of the trachylines have marginal, ex-umbrellar balance organs. The position of the gonads, below the stomach pouches, is a narcomedusan character unless these pouches are actually homologues of the radial canals. Its manubrium suggests trachymedusan rather than narcomedusan affinities.

As an adult animal, *Tetraplatia* is grossly a very differently constructed medusa than any known Narcomedusae, in spite of its obvious narcomedusan nature. The lack of tentacles, radial and ring canals, and the position and structure of the sensory clubs make it unique. The flying buttresses and the swimming lappets also are without counterparts. The extreme reduction of the sub-umbrellar space gives this animal its non-medusan, planuloid shape.

Carlgren (1909) was so impressed by the peculiarities and unusual structure of tetraplatians that he erected a new order of medusae for them, the Pteromedusae, as a group of equivalent rank to the Trachymedusae and Narcomedusae. This action has not been accepted by other workers as a solution to the systematic position of these animals, and, as has been remarked previously, *Tetraplatia* is usually considered to be a narcomedusan. The Narcomedusae contain several unusual forms such as *Polypodium* and *Hydroctena* and some have very unusual, complicated life histories. In general a hydroid phase is absent in their life histories, although all known seem to involve an actinular larval stage. These

actinulae are in general planuloid, tentacled organisms; the tentacles arising at the place on the circumference which demarks the aboral, ex-umbrellar, area from the oral, manubrial area. In the actinula in its simplest form there is no sub-umbrellar region, but as it grows into a medusa the bell margin grows outward and downward, thus creating the sub-umbrellar space. *Tetraplatia* in form and adult structure strongly suggests its actinular affinities and except for the absence of tentacles seems to be a compromise between the structure of actinula larvae and adult trachyline medusae.

There is very little information to guide us to a decision as to what position *Tetraplatia* should have among the Narcomedusae. Mayer (1910) reviewed the several possible classifications within this group, and recognized only two families, the Solmaridae and Aeginidae; the Solmaridae are without stomach pouches while the Aeginidae possess them. Unfortunately Mayer did not consider *Tetraplatia* at any point in his work. Of these two families of Narcomedusae, *Tetraplatia*, by its possession of a pouched stomach, seems to most closely approach the Aeginidae and within this family it would best be placed within the sub-family Cunanthinae.

Within the Cunanthinae can be placed such genera as *Cunantha*, *Hydroctena*, *Cunoctantha*, and *Cunina*. Of these genera *Tetraplatia* would seem to be most closely related to *Cunantha*, although Mayer (1910, Vol. 2, p. 449) said, ". . . the 'genus' *Cunantha* is, I believe, only a developmental stage of Aegina." *Cunantha* is, however, clearly a medusan and does not grossly suggest *Tetraplatia* by its form, but its special features do suggest some of the special features of *Tetraplatia*. For example, the exumbrella bears rows of nematocysts as in *Tetraplatia* and moreover *Cunantha* has only four broad lappets. The stomach pouches of *Cunantha* are very small and only four in number, again as in *Tetraplatia*. The tentacles of *Cunantha* are rudimentary whereas there are none in *Tetraplatia*. If *Cunantha* exists as a

valid genus might not this last character indicate a trend toward loss of tentacles? However, the medusoid form, sensory clubs, numerous statoliths, otoporpae, and gonad ring of *Cunantha* all represent characters quite different from those of *Tetraplatia*.

Broch (1929) in reviewing the classification of the Narcomedusae recognizes three families, the Cuninidae, Aeginidae and Solmaridae. Of the three, again, *Tetraplatia* best fits the definition of the aeginids but at the same time cannot be clearly identified as an aeginid or indeed even as a narcomedusan if one considers its structure and particularly its possession of a statocyst.

Dantan (1925) did not believe that the statocyst of *Tetraplatia* could be considered as derived from the endoderm. Indeed, the whole statocyst is not, nor is it in other trachylines, although the internal cells of the lithostyle are. In *Tetraplatia* it seems to be fairly obvious that the lithostyles, or at least the lithocytes, are endodermal. This character then clearly places *Tetraplatia* among the trachylines. Dantan (1925, p. 452) although disagreeing entirely with Carlgren's classification of *Tetraplatia*, tried to conserve Carlgren's name, Pteromedusae, by making it a family of the Anthomedusae. This was a kind gesture on Dantan's part; however, it is an action contrary to the International Rules of Zoological Nomenclature under which the only allowable family name would have to be Tetraplatiidae if *Tetraplatia* is the type genus.

If *Tetraplatia* is to be placed among the Narcomedusae it will stand out as a very aberrant, highly divergent, form. Its possession of an enclosed lithostyle is a trachymedusan character and the definition of the Narcomedusae would therefore have to be modified to meet this situation. That *Tetraplatia* has strong narcomedusan characters certainly is not to be denied; however, it is an animal that seems to have evolved along a path quite distinct from the normal narcomedusan line. One can hypothesize that *Tetraplatia* is the result of retrogressive evolu-

tion from the aeginid line, or that *Tetraplatia* has evolved directly from primitive narcomedusan ancestors at a point so early that the true medusoid form had not yet been established. If this latter is true, then *Tetraplatia* must represent an early evolutionary experiment in developing a more complex organism than the presumed actinular ancestors of the trachyline medusae. Another suggestion could be that *Tetraplatia* represents a neotenic actinula, and as such might better be called aberrant than primitive. Regardless of which of these hypotheses one might subscribe to, I feel that the unusual characteristics of *Tetraplatia* place it in a position between the two recognized orders of trachyline medusae and that it is morphologically so distinct that it deserves to be placed in an order of its own. I therefore subscribe to the classification proposed by Carlgren (1909) and recognize *Tetraplatia* as a pteromedusan. Further light may be shed on the actual ancestry of *Tetraplatia* once its development and complete life history are known.

The distribution of *Tetraplatia* in the Eastern Pacific, as indicated in Figure 4, presents a pattern in the northern latitudes which one might predict on the basis of known ocean currents. That is, this animal seems to live in the water which slowly moves in a clockwise direction and makes up the North Pacific Current. On this basis one can predict that *Tetraplatia* can be expected to be found throughout this whole current system including the Kuroshio and the North Equatorial Current. Komai (1939) has already reported four specimens from Japan. Further collecting alone will test this suggestion. However, if one examines Figure 4, it will be seen that there is a considerable gap between the most southerly point at which *Tetraplatia* was collected and the main area from which most specimens were taken. That is, no specimens were collected between 5° south latitude and 20° north latitude. The area covered by the lack of specimens was sampled by the Scripps Institution cruise "Shellback" and the

specimens taken at 20° N. and 5° S. were from that expedition. Although not all of the plankton tows taken on "Shellback" have been examined by the writer, 18 samples spaced throughout the gap have been examined and no *Tetraplatia* were found. The tows in this area were oblique hauls with a one-meter net fishing from 300 meters depth to the surface. The presence of one specimen of *Tetraplatia* at 5° S. suggests that *Tetraplatia* is present in the cooler waters of the South Pacific, since this specimen was from the northern end of the Peru Current, a cold water mass moving in a counter-clockwise direction. The gap between this cold water mass and the cold water of the North Pacific is filled with the warmer waters of the Equatorial Counter Current and *Tetraplatia* may be unable to live in this area of warmer water. This, perhaps, explains the absence of *Tetraplatia* in the area under consideration, although a possible alternative solution might be in the fact that colder waters underlie the area and *Tetraplatia* may be found there if samples are taken from the deeper waters. If this is so, then the lack of *Tetraplatia* may be an artifact of sampling and the result of tropical submergence as this animal stays in the colder waters which may offer to it a more suitable environment.

CONCLUSION

Tetraplatia volitans is considered, by the author, to be a highly specialized and divergent trachyline medusan of narcomedusan ancestry which has evolved a trachymedusan sense organ. Its adult morphology seems to represent a compromise between the structures of actinula larvae and adult narcomedusans. Its highly specialized lappets and new features such as the flying buttresses and enclosed adoral lithostyles represent unique characters. In order to give proper weight to the unusual nature of this animal, Carlgren's order of Pteromedusae is recognized as a valid classification. *Tetraplatia* is nearly worldwide in distribution and may be characterized as a

holoplanktonic organism which undergoes diurnal vertical migrations.

REFERENCES

BROCH, H. 1929. Trachylinen (Trachymedusen und Narcomedusen). *Nord. Plankton* 6: 481–540.

BUSCH, W. 1851. *Beobachtungen über Anatomie und Entwicklung einiger wirbellosen Seethiere.* 143 pp. August Hirschwald, Berlin.

CARLGREN, O. 1909. Die Tetraplatien. *Wiss. Ergeb. der Deut. Tiefsee—Exped.* 19 (3): 77–122, pls.

CLAUS, C. 1878. Ueber Tetrapteron (Tetraplatia) volitans. *Arch. f. Mikros. Anat.* 15: 349–359, 1 pl.

DANTAN, J. L. 1925. Contribution a l'Étude du Tetraplatia volitans. *L'Institut Óceanog., Ann.* (n.s.), 2: 429–459, 12 text figs., 2 pls.

——— 1927. Tetraplatia volitans (Busch, 1851). *Faune et flore de la Méditerrannée.* 1à7, [1–pp.], 2 figs. Institut Óceanographique, Paris.

FEWKES, W. J. 1883. The affinities of *Tetraptera volitans. Amer. Nat.* 17: 426.

HAND, C. 1954. Three Pacific species of "Lar" (including a new species) their hosts, medusae and relationships (Coelenterata, Hydrozoa). *Pacific Sci.* 8 (1): 51–67, 7 figs.

HAECKEL, E. 1879. *Das System der Medusen.* 672 pp., Gustav Fischer, Jena.

HYMAN, L. 1940. *The invertebrates, Protozoa through Ctenophora.* xii + 726 pp., 221 figs.

McGraw-Hill Book Company, Inc., New York.

KOMAI, T. 1939. On the enigmatic coelenterate Tetraplatia. *Jap. Jour. Zool.* 8: 231–250, 11 figs., 1 pl.

KROHN, A. 1853. Ueber die Entwickelung der Seesterne und Holothurien. *Arch. f. Anat. u. Physiol.* 1853: 317.

——— 1865. Ueber *Tetraplatia volitans. Arch. f. Naturgesch.* 1: 337–341.

KRUMBACH, T. 1924. Scyphozoa. In *Handbuch der Zoologie* Vol. 1, 1060 pp., Walter De Gruyter and Co., Berlin.

LELOUP, E. 1935. Contribution a la répartition de *Tetraplatia volitans* (Busch). *Brussels Mus. Roy. d'Hist. Nat., Bul.* 11 (4): 1–7.

LEUCKART, R. 1866. Bericht über die Wissenschaftlichen Leistungen in der Naturgeschichte der Niederen Tiere während d. Jahre 1864 u. 1865. *Arch. f. Naturgesch.* 2: 99–100.

MAYER, A. G. 1910. The hydromedusae. In *medusae of the world.* Vol. 1, 230 pp. Carnegie Institution, Washington. [Pub. 109 of the Carnegie Institution.]

PAPENFUSS, E. 1936. The utility of nematocysts in the classification of certain Scyphomedusae. I. *Lunds Univ. Årrskr.*, N. F., Avd. 2, 31 (11): 1–26.

ROSE, M. 1926. Le plankton de la baie d'Alger pendant le mois de janvier. *Soc. d'Hist. Nat. de l'Afrique du Nord, Bul.* 26: 57–62.

RUSSELL, F. S. 1938. On the nematocysts of hydromedusae. *Mar. Biol. Assoc., U. K., Jour.* 23: 145–165.

VIGUIER, C. 1885. Sur le Tétraptère (Tetraplatia volitans) Busch. [*Paris*] *Acad. des Sci., Compt. Rend.* 100: 388–390.

——— 1890. Études sur les animaux inferieurs de la baie d'Alger. Le Tétraptère (Tetraplatia volitans Busch). *Arch. de Zool. Expt. et Gén.* II, 8: 101–142, 2 pls.

WEILL, R. 1934. Contribution a l'etude des Cnidaires et de leur nématocystes. *Wimereux, Sta. Zool., Trav.*, 10: 1–347; 11: 348–701.